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THE ANATOMY OF THE NORTH AMERICAN CONIFERALES TOGETHER WITH CERTAIN EXOTIC SPECIES FROM JAPAN AND AUSTRALASIA. PART I.

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INTRODUCTORY.

THE present work had its origin in 1880, in an attempt to construct a system of classification for the North American Coniferæ, based upon the anatomy of the vascular cylinder of the mature stem. The fundamental idea was that such a classification would prove of great value in the identification of material used for structural purposes, but investigations had not been carried very far when it became manifest that some such arrangement was imperatively demanded in other directions and for purposes of a more strictly scientific character. In entering upon the study of fossil plants it was recognized that the most fruitful source of reliable data must be found in the stem structure. At that time there was little in the way of an adequate basis for further study of this sort, inasmuch as the current diagnoses of the vascular structure were found in most cases to be singularly inadequate, and often so incorrect as to require exten-

sive revisions. It was furthermore found that, in order to reach correct conclusions in the case of stems which must often present marked structural alterations arising through the influence of decay and other conditions attending fossilization in its various forms, it was indispensable that there should be a trustworthy means of comparison with existing types, whereby sources of error arising from eliminated structures might be definitely excluded, and the fossil referred with certainty to its nearest relative. The original intention was therefore modified with a view to meeting the requirements of palæobotanical research. During the twenty odd years these investigations have been in progress, there has been much change in the views held by botanists respecting the significance of anatomical features as affording evidence of descent, and our own studies brought forth facts which gave repeated emphasis of the most positive kind, to the idea that questions of phylogeny cannot be settled either by the morphologist in the narrower sense or the physiologist, either separately or combined, and that a proper historical point of view can be gained only when to such labors we join the data derived from a critical study of the stem structure in all its details. As the greater may always be held to include the less, the present discussion is to be regarded primarily from the biological point of view, and questions of descent will take precedence over those of mere taxonomy.

The original intention was to make a complete study of all the North American woods, comprising, as enumerated by Sargent in his report in the *Tenth Census of the United States*, some four hundred and nineteen species and varieties; but the great importance of the Coniferæ from an economic point of view, their frequent representation in the fossil state and their relatively more simple structure, eventually led to their selection as the one group in which initial studies might be prosecuted with the most immediate and profitable results. While the North American species constituted the original basis, various exotic species were added from time to time with the result that our studies as now completed, comprise ninety-two species from North America, twenty-one species from Japan, and four species from Australasia. This extension has proved of great value, not only from a

palæontological point of view, but also because of the important bearing such exotic types have had in the solution of questions relating to descent. The methods adopted in these investigations have already been fully explained (38, p. 33 *et seq.*) and further details at this time are uncalled for.

In 1896 the work had reached such a point that it was deemed desirable to make a preliminary statement of results. This appeared in a paper published in the *Transactions of the Royal Society of Canada* entitled the "Generic Characters of the North American Taxaceæ and Coniferæ," in which it was shown that generic differentiations were possible. The diagnoses and artificial key to the genera thus published, have been in constant use since that time for the determination of fossil species, with the most gratifying results; and after seven years of severe testing, and in the light of more extended studies, they are found to be substantially correct and reliable.

The question of specific differentiation presented a far more difficult problem, the solution of which has now been reached as embodied in the present work.

In the prosecution of these studies I have been under deep and often constant obligations to helpful friends working along other lines. To Prof. C. S. Sargent of the Arnold Arboretum, as also to Mr. Morris K. Jesup, President of the American Museum of Natural History; Dr. N. L. Britton, Director of the New York Botanical Gardens; the late Baron Ferd. von Mueller of Melbourne, Australia; Sir W. T. Thistleton-Dyer, Director of the Royal Gardens, Kew; and to Mr. E. J. Maxwell of Montreal I am indebted for much valuable type material. To Dr. B. E. Fernow, formerly Chief of the Bureau of Forestry of the United States Department of Agriculture, I am under obligations for a large amount of material specially selected with reference to testing the accuracy of diagnoses and details of the key. To Mr. J. G. Jack of the Arnold Arboretum, I am under particular obligations for the readiness with which he has frequently responded to requests for material of a trustworthy character, and his care in selecting a large series of specimens for testing purposes, which have contributed very largely to the success of the final results. To my assistant,

Miss C. M. Derick, I wish to extend my appreciation of the frequent and valuable assistance she has rendered.

SPIRAL TRACHEIDS.

In the genesis of the vascular system, the elements first differentiated from the generative tissue, constitute the primitive elements now generally recognized in accordance with the designation of Russow as protoxylem. These elements are tracheids, and in the Coniferales as also in the Ginkgoales, they always occupy a position immediately external to the pith and therefore on the inner face of the zone representing the growth of the first year, but they are not repeated in the formation of xylem structure in subsequent years. The primitive character of such tracheids is therefore indicated, not only by their position and relation to development of other parts, but it is also exhibited by their occurrence in plants where the vascular system is of a far more simplified type and of which they constitute relatively more prominent features. In the Equisetineæ, both fossil and recent, they are conspicuous elements of the vascular structure, being found within the limits of the carinal canal. They similarly occur in the Ophioglossaceæ and elsewhere among the more primitive of the vascular plants. The general evidence, then, which may be derived from a comparative study of various types, tends to enforce the idea that, originating as a primitive form of the wood structure, and more or less common to all the vascular plants, they are relatively predominant in the lower forms, with a tendency to obliteration through replacement or modification in the higher types, where their presence may be held to represent a survival of ancestral characters. This view gains additional support from a study of the peculiar structural variations which characterize such tracheids, and the progressive modifications which they have been found to undergo in relation to the development of the secondary xylem.

The protoxylem elements are distinguished by the presence of thin, spiral bands disposed upon the inner surface of the primary wall in such a manner as to afford a substantial measure of mechanical support. These ribbon-like bands represent second-

ary growth in thickness of a local nature — the localization being determined with reference to the requirements of such support in the first instance. De Bary (9, p. 57) has shown that they exhibit considerable variety in the number of fibres and the direction and steepness of the coils. Their number is often only 1–2 in narrow tubes which are first formed when the differentiation of tissues begins, in others 4 or more, and it rises in many cases in the angiosperms to 16–20. He has furthermore pointed out that the steepness of the coils is greatest in those tubes which are developed earliest, before the extension of the part to which they belong has ceased; since in these the coils are separated from one another by the extension which the tube itself undergoes. These facts appear to suggest that the more typical the spiral tracheid is, the more fully does it emphasize the idea of a primitive structure; but that as the spirals become more dense or closer, there is a tendency toward more uniform and less localized secondary growth of the wall, as expressed in the structure of the higher types of plants or the secondary xylem elements of the Coniferæ. In confirmation of such a view, reference may be made to the commonly observed fact that the spirals tend to a more compact arrangement at the ends of the elements, becoming correspondingly more open in the central region; and likewise to the well known transitional forms which these structures exhibit, whereby their original characteristics are completely lost as they merge ultimately into tracheids devoid of spirals, but characterized by the presence of pits of various forms. In 1840, Don (52) pointed out that the tracheids of *Cycas revoluta* exhibit scalariform structure at one end and bordered pits at the other. This fact has more recently been commented upon by Williamson who observed the same fact independently, and drew from it the inference that a definite relation exists between the scalariform markings and the pit structures of such a nature that the one is the natural successor of the other. In *Ginkgo biloba* which is now generally conceded to represent a much more primitive type than the Coniferæ, though more advanced than the cycads, precisely similar transformations are to be met with. The evidence of fossil plants is quite as convincing as that derived from existing

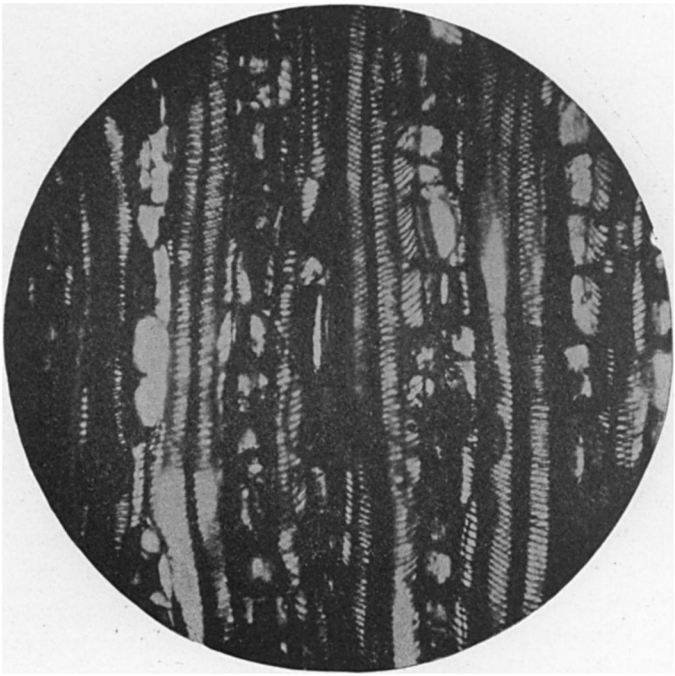


FIG. 1.



FIG. 2.

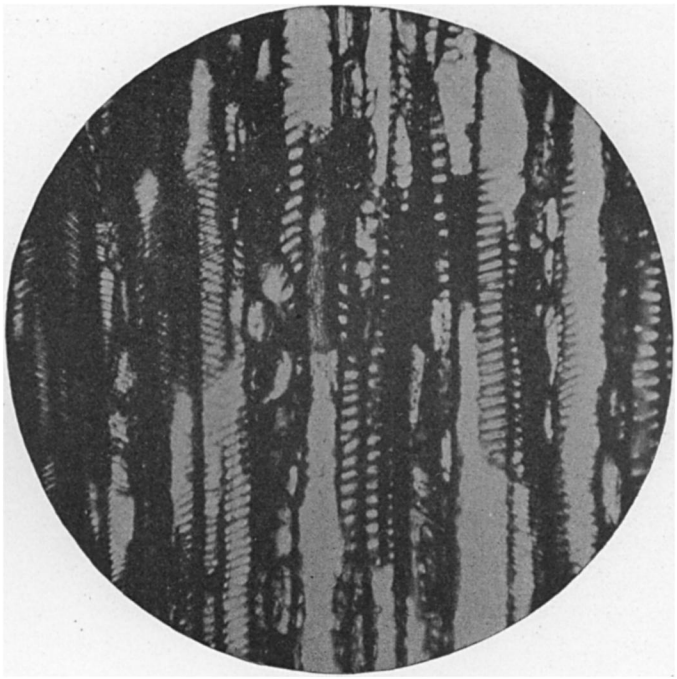


FIG. 3.

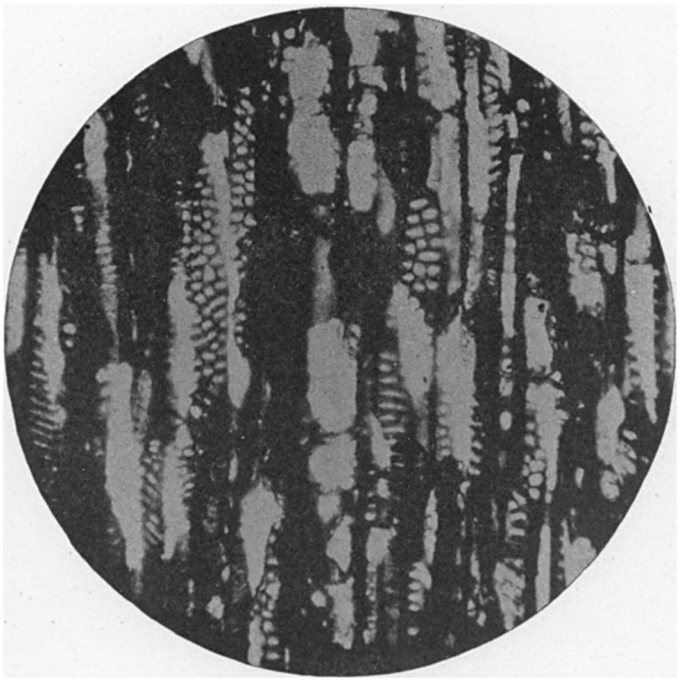


FIG. 4.

FIGS. 1–4.— *Cordaited brandlingii*. Radial series showing the origin of bordered pits from spiral tracheids. × 180.

species, while it is often of distinctly greater value because affording data derived from presumably more primitive types. Thus such transitions are well known, though of a relatively simplified form in the structure of the calamitean stem, and an excellent example of this kind is afforded by a figure given by Scott (43, p. 22). In 1869 Williamson (52, p. 69) directed attention to the occurrence of such transformations in the tracheids of Cordaites (Dadoxylon). A more recent study of this genus (39, p. 57 and 43, p. 418) has shown that this feature is well exhibited in *C. brandlingii*, where a suitable radial section (Figs. 1–4) will present a more or less graduated series of transitions from the typical spiral tracheid of the protoxylem, through scalariform structures to the multiseriate bordered pits of the tracheids in the secondary xylem; while within the limits of the same tracheid, such transitions may be observed as it were, in process of development, affording the most conclusive proof in this respect. These transitions as observed in *Cordaites brandlingii* show the following phases:

In the successive radial development of new tracheids, there is a constant tendency to a more uniform thickening of the cell wall by secondary growth. This at first finds expression in the more compact arrangement of the spirals which later coalesce at various points, thus giving rise to more localized areas devoid of secondary growth, and hence to a scalariform structure in which the general lines conform more or less exactly, to the direction of the original spirals. By a further modification the elongated, thin areas become converted into shorter, often isodiametric areas substantially by a process of division. A further tendency to general thickening of the walls causes the margins of the scalariform structure to project from all sides and extend over the area of arrested growth as a lip which never completely closes at the centre, where there is left a usually circular, sometimes oval or again lenticular or even oblong opening, and in this manner the bordered pit is formed.

The region within which these changes occur, or the "transition zone," is subject to great variation whereby the change from spiral to bordered pit may arise very gradually through a broad radial zone, as in *Cordaites brandlingii* or it may occur very

abruptly as in the modern Coniferæ. The general tendency of such evidence is to show that with a higher type of organization, there is a corresponding diminution in the transition zone and increased abruptness in the structural alterations. The logical result of an extension of this process would be the reduction of the bordered pit to the condition of a simple pit, and ultimately, its complete obliteration. In the Coniferæ the reduction of the bordered pit to the condition of a simple pit sometimes occurs in the case of medullary rays or even in the case of tracheids with very thick walls, but it becomes most prominent in the angiosperms where it is a characteristic feature. Instances also occur in some of the hard pines, in which the pit is completely obliterated. This applies in particular to tracheids of the summer wood, the walls of which have become unusually thickened.

The relations to which attention has thus been directed somewhat in detail, have been expressed in more general terms by De Bary (9, p. 321) in the statement that "Outside the primitive elements, wider trachæ follow. Their development takes place successively, advancing from the inner edge of the bundle outwards, and as a rule at a time when the elongation of the entire part to which they belong is nearly at an end. The thickenings on their walls therefore have a successively denser arrangement: dense spiral and annular trachæ, then reticulated and pitted trachæ follow one another in succession from within outwards, with gradual transitions, or with the omission of one or the other immediate form." It is probably a justifiable inference from the preceding facts that, the relation which exists between the spiral tracheids of the protoxylem and the pitted tracheids of the secondary xylem in the Coniferæ, is, in general terms and from the standpoint of development, the same as that exhibited between the lower and higher types of vascular plants.

Accepting the general principle which appears to be justified by the foregoing facts, that the transition from spirals to bordered pits is a feature in development which bears a direct relation to the evolution of higher types of organization, we may utilize it for the purpose of determining the general phylogeny of the Coniferæ so far as they may show a survival of such characters. Out of a total of 117 investigated species of indigenous

and exotic Coniferæ, 9.4% show a more or less permanent survival of the spiral structure within the limits of the secondary xylem. Of these 6% fall within the Taxaceæ (Torreya 3.45%, Taxus 2.5%), while in the Coniferæ the remainder is divided between Pseudotsuga (1.7%), Larix (0.86%) and Pinus (0.86%). In the genus Torreya the spirals are, on the whole, rather open and distinguished by being 2–4 sèriate. They are typical throughout the spring wood, but in the thin summer wood they quickly become vestigial and ultimately disappear altogether. In *T. taxifolia* there is also a marked condensation whereby the spirals are all brought into a more compact series within the earlier tracheids of the summer wood. All of these changes appear to be directly related to a progressive increase in the thickness of the tracheid wall.

In all investigated species of Torreya, there is a rather wide variation in the angle which the spirals make with the axis of growth, and this becomes most pronounced in *T. californica*, which gives the lowest angle for any species of either Torreya or Taxus. Usually the spiral has an angle quite distinct from that of the lines of striation in the cell wall, but in *T. taxifolia* the two often coincide. The following will show the various details derived from the average of ten measurements for each species.

	Average angle.	Highest angle.	Lowest angle.	Extreme range.
Torreya nucifera	70.5	87.0	57.0	30.0
" *taxifolia*	70.4	77.0	61.0	16.0
" *californica*	46.2	63.0	30.0	33.0
Means	62.3	75.7	49.3	26.3

In the genus Taxus, the spirals are rather close and in 2, rarely 3 series. As in Torreya they are typical throughout the spring wood, and show a pronounced tendency to obliteration in the summer wood. This tendency is subject to considerable variation in different species. In *T. canadensis* the spirals are conspicuous throughout. In *T. floridana* they usually disappear

in the later growth and are wholly wanting in the two or three, last formed tracheids. In *T. brevifolia* they become very imperfect in the outer summer wood and tend to disappear completely, only vestiges remaining in the last formed tracheids. In *T. cuspidata* the spirals are generally absent from the summer wood, or when present, they are merely vestigial. The angle is somewhat greater —about 7 deg.— than in Torreya, and this fact is apparent with respect to certain species without special measurement. The four species appear to be paired off in such a way as to represent a mean difference of about 10.9 deg. as between *T. canadensis* and *T. floridana* on the one hand, *T. brevifolia* and *T. cuspidata* on the other. In all cases the angles of the spirals are quite distinct from those of the lines of striation. The following details are based upon the average of ten determinations.

	Average angle.	Highest angle.	Lowest angle.	Extreme range.	Mean of 2
Taxus canadensis . . .	72.4	88.0	66.0	22.0	
" *floridana* . . .	78.4	90.0	72.0	18.0	75.4
" *brevifolia* . . .	63.0	76.0	55.0	21.0	
" *cuspidata* . . .	66.1	87.0	45.0	42.0	64.5
Means . . .	69.9	85.2	59.5	25.7	

A comparison of these results in detail emphasizes the fact that the distribution of the spirals, as between spring and summer wood, is in direct harmony with the principles already stated, and furthermore, that the angles at which the spirals develop do not afford an adequate basis for generic differentiation. It is nevertheless possible to recognize sub-generic groups in such wise that in both genera a general line of division may be established at 70 degrees. In the case of *Torreya californica*, the very low angle of 46.2 degrees may be regarded as a differential character of specific value.

In the genus Pseudotsuga, spirals are confined to the tracheids of the spring wood. This has a partial exception in *P. macrocarpa*, in which vestigial spirals may be observed in the earlier tracheids of the summer wood. In this species the mean

angle is 70 degrees, but the spirals are always characterized by lack of prominence, they are often widely distant, and the somewhat extended areas within which they are wholly wanting or fragmentary, suggests a process of obliteration. In *P. douglassi* the average angle is 82 degrees; the spirals are characterized by considerable prominence and they are also, on the whole, close. In this genus these two factors obviously possess a well defined differential value with respect to the two species.

Among the higher genera only two cases are known in which spirals occur, but in each the character is of a very sporadic nature. In *Larix americana* spirals are frequently found in the summer wood, but they are so inconstant in their occurrence, and they present such varying aspects, that the angle cannot be determined. In *Pinus tæda*, where the walls of the summer tracheids are very thick, rudiments of spirals may sometimes be seen. Here also it is manifestly impossible to determine the angle.

Viewing these five genera collectively, their spirals conform fully, in their occurrence and relation to progressive development, to the general principles already stated, and especially as formulated by De Bary. They possess no differential value of generic rank with respect to Pinus and Larix, but they do have such value with respect to Torreya and Taxus on the one hand, and Pseudotsuga on the other, the differentiation resting upon their occurrence in the summer wood in the former, and their exclusion from that region in the latter. Were any question to arise in this connection, it could be authoritatively decided by the definite association of resin passages and fusiform rays in Pseudotsuga.

It only remains for us to ascertain how far such structural features may be employed as a basis upon which to determine the general phylogeny of the genera. As between Torreya and Taxus there is very little upon which to base conclusions respecting sequence in development, and it is apparent that both of these genera have attained to nearly the same level. Such differences as do exist, however, seem to point to the relatively, though slightly, inferior position of Torreya as indicated by (1) the smaller angle in that genus and (2) the generally more com-

pact spirals of Taxus. This fact, so far as it possesses phylogenetic value, appears to confirm the conclusions as to the relative positions of these two genera, already determined upon the basis of external morphology as stated by Eichler (11, p. 108).

It has already been made clear from the preceding facts, as well as from former discussions (40, p. 56) that in the case of the Taxaceæ and also of Pseudotsuga, the spirals must be regarded as a survival of primitive structures. On a former occasion (40, p. 57) I was inclined to consider that their occurrence in Larix and *Pinus tæda* was atavistic, but in the light of more recent evidence as now set forth, this opinion requires modification in so far as to include the idea that they do not express mere parallelisms in development, but that they afford evidence of a common ancestral type at some point far anterior to the evolution of the Taxaceæ. We must therefore consider that Torreya, Taxus, Pseudotsuga, Larix and Pinus represent different branches of a general phylum — undoubtedly including also, other closely related genera in which the spirals have been wholly obliterated — which had its origin at a point anterior even to such types as Cordaites, and therefore, in all probability in what Coulter (7) has very happily designated as "the great Cordaitean plexus" arising from the eusporangiate ferns, or what, according to our more recent knowledge, and Coulter's more recently expressed view (8, p. 172) would be designated as the Cycadofilices.

Bordered Pits Distribution and Structure.

In the preceding pages, the derivation of the bordered pit from the spiral tracheid, and its obviously more intimate relation to a higher type of development have been made clear. Our present purpose is to discuss these structures with special reference to (1) occurrence, (2) distribution, (3) structural modifications, (4) taxonomic value and (5) their value as evidences of descent.

At the outset, reference may be made to the occurrence of bordered pits on the radial walls of the ray cells as exhibited typically in Sequoia and Taxodium. Their location in such situa-

tions, as also upon the radial, terminal, upper and lower walls of the ray tracheids may be held to represent a feature somewhat distinct from their presence on the walls of the wood tracheids, and their consideration properly belongs to a discussion of the medullary ray as a whole; but it may be observed that they constitute a characteristic feature in the structure of the ray elements in the great majority of the Coniferales.

The occurrence of bordered pits on the walls — especially the radial walls — of the wood tracheids in the Ginkgoales and Coniferales, is much too familiar a fact to call for special discussion at this time, but reference may be made to the additional fact that their characteristic structure is such as to permit of their use for the general purpose of tracing possible lines of descent through such extinct types as Cordaites and the Cycadifilices. It is true that similar bordered pits originating in modifications of spiral structures, are to be met with, often in great numbers, in the higher angiosperms, but in such cases the associated structures permit of a clear and definite differentiation of all such woods from the Coniferales.

Radial walls.— The characteristic situation of the bordered pits is on the radial walls where, as was shown many years since by De Bary (9, p. 160), "the pits of contiguous tracheids always correspond to one another in such a way that on each limiting surface, all the cavities of the pits of one fit exactly over those of the other. The plano-convex cavities are thus applied to one another in pairs so as to form the lens-shaped pit cavities" as seen in tangential section. But on surfaces abutting on elements of another order, *e. g.*, parenchyma cells, the bordered pits of the tracheids correspond to non-bordered pits, or they are opposite an unpitted wall. Four typical variations of the bordered pits may be recognized: — (1) the multiseriate, when they are disposed in any number of rows more than two, (2) the 2-seriate, (3) the uni-seriate with occasional pairs of pits, and (4) the strictly uni-seriate. The general sequence thus presented will be found to be in direct accord with the evolution of higher types of structure and organization.

The most primitive type of gymnosperm presenting a multiseriate arrangement, is the genus Cordaites. Among eleven

species of this genus which have been critically studied within recent years (39) there is a general agreement in the constancy of this character which thereby becomes of generic value. In all the species the pits are disposed in such a compact manner throughout the entire extent of the tracheid, as to present a hexagonal outline. In *Cordaites acadianum*, they are 2–5-seriate (Fig. 5). In other species they vary from 2-seriate in *C. hamiltonense* and *C. newberryi* (Fig. 6) to occasionally 4-seriate in *C. clarkei*. In the majority of species, the rows are not constant, but show a varying number from 1 to 3, or 2 to 5, this variation

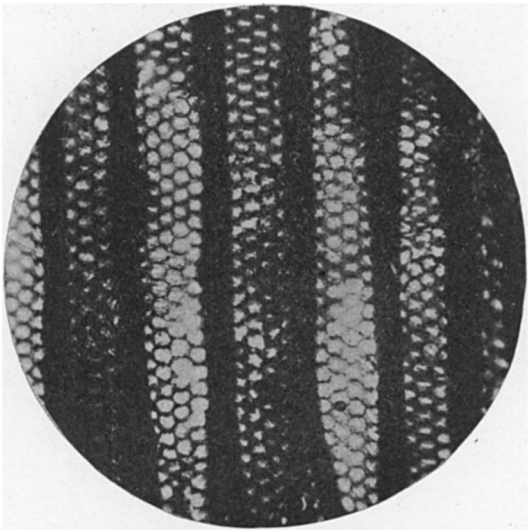


FIG. 5.— *Cordaites acadianum*. Radial section showing disposition of the bordered pits. × 180.

being exhibited by adjacent tracheids in accordance with the variation of the latter in radial diameter; and viewing this distribution as a whole, it cannot be doubted that it represents corresponding differences in development. One of the most striking features of the genus is to be met with in *C. newberryi* (Fig. 6), which is unique in the segregation of the pits into groups of 6–13.

In Araucarioxylon Knowlton has shown (25, p. 614) that, while conforming to the characteristic form and compact arrangement presented in Cordaites, the pits exhibit far less constancy in their serial arrangement, and in this respect they are at once

comparable with those of the existing Araucarias. Among the latter, *A. cunninghamii* shows a 1–3-seriate disposition; *A. excelsa* is 1–2-seriate while *A. bidwillii* is strictly 1-seriate. All

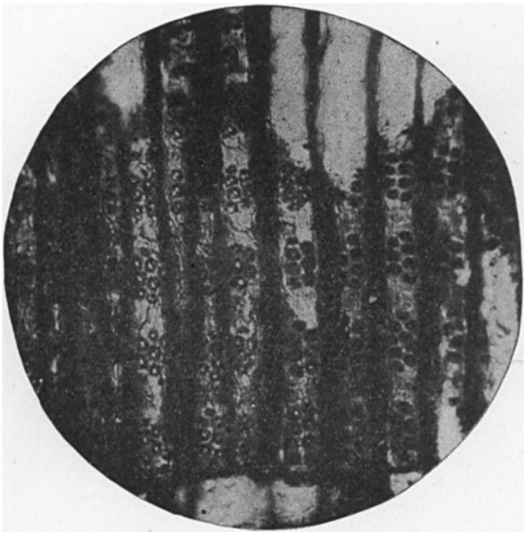


FIG. 6.— *Cordaites newberryi.* Radial section showing disposition of the bordered pits. × 180.

of the extinct species as comprised in the genus Araucarioxylon not only show similar variations, but such variations are found to cover a much wider range. A comparison of all the species, both recent and extinct, now available for that purpose, is of interest in this connection.

	1-ser.	2-ser.	3-ser.	4-ser.
A. bidwillii	x			
wurtembergianum	x			
schmidianum	x			
hugelianum	x			
excelsa		x		
arizonicum		x		
edvardianum		x		
virginianum		x		
doeringii		x		
subtile		x		
argilliacola			x	
heerii			x	
cunninghamii			x	
robertianum				x

Such a comparison brings into strong relief the fact that the Araucarias, both past and present, constitute a transitional group with a somewhat wide range of variations, and in this respect they may be said to stand between the more stable Cordaites and Agathis on the one hand, and the far more variable Coniferæ on the other, since in *Agathis australis* we find essentially the same features of structure and distribution as in Cord-

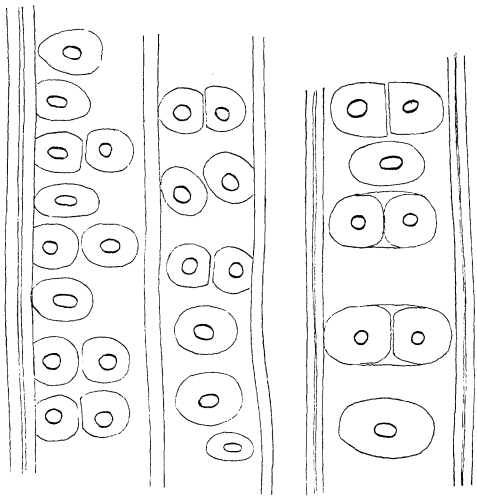


FIG. 7.—*Pinus cubensis.* Radial section showing the form and disposition of the bordered pits. × 280.

aites, the pits being 1–3-seriate. The sequence presented above may be held to be in the inverse order of development, and *A. robertianum* must therefore be held to represent the most primitive form.

It is apparent that in Cordaites, Araucaria (including Araucarioxylon) and Agathis, the pits are invariably distinguished by two constant features; (1) their hexagonal form and (2) their very compact disposition throughout the entire extent of the tracheid. They often deviate from the multiseriate arrangement typical of the group as a whole, in that in individual cases they are reduced to a 1-seriate arrangement. They thus tend to overlap the next group which is distinguished by a 2-seriate disposition, but any confusion which might arise from this cause, may be overcome by reference to the special form and dis-

position of the pits as will more fully appear in the following lines.

Among the remaining Coniferales, 20 species of various genera, or 17.2 % in all, show a 2-seriate arrangement, and to this group we must also add the Ginkgoales and various fossil species. Here the multiseriate disposition of the pits involves features which at once distinguish the group as a whole from the preceding, clearly placing it upon a higher plane of development. The pits are never hexagonal but generally elliptical or round, while they also show a strong tendency to extreme segregation. When brought into a compact arrangement as in Cupressoxylon, Sequoia or various species of Pinus, they are flattened only along the lines of limited contact, which are usually confined to one end (Fig. 7). A very characteristic feature of this group is the further fact that the 2-seriate arrangement is not constant, either in the same section or in the same tracheid. Both *Pinus tæda* and *P. cubensis*, as also *Larix americana* and *Tsuga canadensis* afford illustrations that while typically 2-seriate, a given section may show a strictly 1-seriate arrangement, and this difference also obtains as between contiguous cells. In all such cases examination will show that the variation is directly related to the relative size of the tracheids in such a way that the narrower tracheids, or those arising from a less vigorous growth, are 1-seriate. Within the individual tracheid there is a strong tendency to a 1-seriate arrangement in the central region, while it is 2-seriate at the extremities; and this law holds so true that in those species which are exceptionally 2-seriate, judgment should be reserved until it is seen that the 1-seriate form holds throughout.

The antithesis of the multiseriate type is found in the 1-seriate form. This is typical of 50 % of all the species included in the present studies. In such cases the form of the pit is never hexagonal or specially flattened. When the disposition is somewhat compact, as in *Pinus strobus* (Fig. 8), the outline becomes more or less strongly elliptical, but as the segregation is more pronounced, a definitely circular form prevails (Fig. 9). Within the limits of the individual tracheid the same law of distribution obtains as in the 2-seriate type, whereby segregation is always most pronounced in the central region.

Between species of the strictly 1-seriate, and those of the strictly 2-seriate type, there is an intermediate or transition group comprising 34 species, or 29.3 % of the investigated species, into which members of the first two groups may occasionally be projected. The distinguishing feature of this group is the occurrence of pits in pairs which are usually distant, and in no case so numerous as to distinguish a 2-seriate disposition. They give undoubted proof of the passage from one type to the other. Like the 2-seriate type, this feature is not confined to any one genus or to any particular group of genera, but it applies with equal force to any genus, the members of which may therefore represent any or all of the three types here specified.

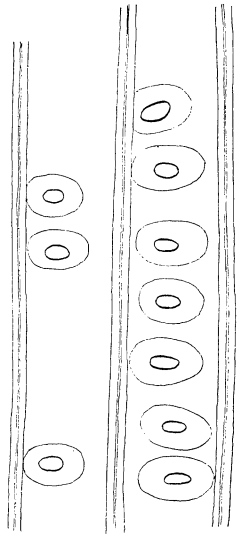


FIG. 8.— *Pinus strobus*. Radial section showing the form and disposition of the bordered pits. × 280.

Viewing the distribution of the bordered pits from the standpoint of zonal development, it is found to be universally true that, in the earlier spring wood there is the strongest tendency to a multiseriate arrangement. With a radial increase of the xylem, this tendency constantly diminishes, with the general result that the pits become more strictly uniseriate and more distant toward the summer wood in which they are sometimes wholly obliterated — this being the case when the cell wall acquires unusual thickness.

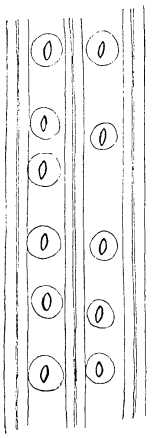


FIG. 9.— *Pinus strobus*. Radial section showing the bordered pits of the summer wood. × 280.

Upon careful examination, the foregoing facts will be found to be in exact accord with the law formulated by De Bary with reference to variations in the structure of spiral tracheids and the genesis of bordered pits as already stated. In accordance with this law it is possible to conclude that relatively rapid growth is coördinated with a primitive development, while the converse

is true of a slow rate of growth which is again convertible into terms of maturity. On this basis we may present the following general outline of sequence in development, as preliminary to further and more detailed discussion of phylogeny.

Cordaites.	2–5 seriate, hexagonal pits.	Compact throughout the tracheid.
Araucarioxylon.	1–4 " " "	
Araucaria.	1–3 " " "	
Agathis.	1–3 " " "	
Ginkgo.	1–2 " round or oval pits.	More or less, often strongly segregated.
Higher Coniferales.	1–2 " " " " "	
" "	1–ser. & pairs " " " "	
" "	1–seriate. " " " "	

Tangential Walls. — The occurrence of bordered pits on the tangential walls is a well-known and characteristic feature of the Coniferales. In the case of fossil forms, to which Araucarioxylon offers a partial exception, it cannot be satisfactorially demonstrated because of the peculiar alterations of the cell wall, but that it is present we are permitted to infer from analogy with existing species upon which dependence must be placed for an elucidation of the general law. The typical position for such pits is upon the tangential walls of the summer wood, where they are most satisfactorily seen in radial section, inasmuch as they are always readily observable when present, and their most essential features are displayed in a manner not possible in a tangential section (Fig. 10). Pits occur in this position in 71.7 % of all the investigated species, and their absence in 28.3 % points to some special features in development which may be assumed to have a general bearing upon the question of descent and relationship. In Agathis, as represented by the one species, *A. australis*, such pits are a prominent and characteristic feature, but in the nearly related Araucaria, they are remarkable for their uniform absence. In the primitive Ginkgoales they

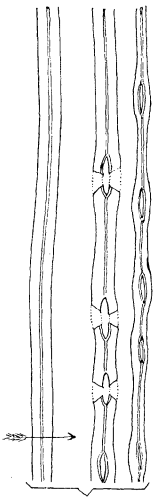


FIG 10 — *Sequoia gigantea*. Radial section showing the bordered pits on the tangential walls of the summer wood. × 280.

are also present, but among the Taxaceæ, while generally present, they are occasionally wanting as in *Torreya taxifolia* and *T. nucifera* or 66.6 % of the investigated species of that genus. Nowhere else among the Coniferales do we find such a feature until we reach the genus Pinus, the second and higher section of which is invariably characterized by their absence, thus presenting an exceptional feature to the extent of 68.3 % of that genus. That such absence represents a process of obliteration conformable to De Bary's law cannot be doubted, while the sporadic recurrence of this feature in often widely separated genera, or in particular species of a given genus, must be held to have a more or less direct bearing upon the general course of development. This is emphasized by the observation that in *Larix americana* and *L. leptolepis* as also in *Picea bicolor*, there is a more or less pronounced tendency to an obliteration which is never fully developed. This is expressed in the somewhat remote position of the pits and their very small size, which renders them obscure and often difficult to discover. In this respect these species represent transitional forms.

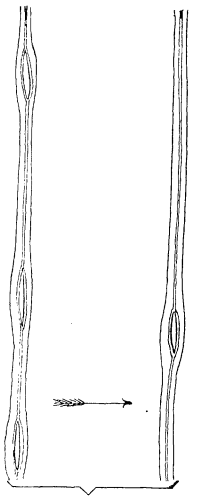


FIG. 11.—*Sequoia gigantea.* Radial section showing the bordered pits on the tangential walls of the spring wood. × 280.

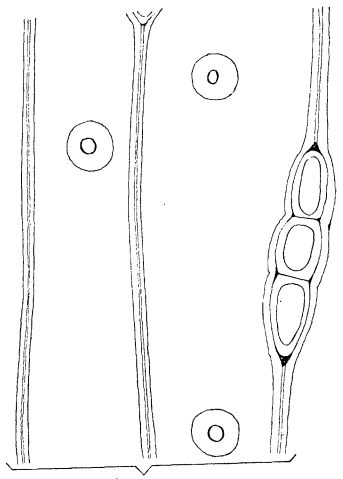


FIG. 12.—*Sequoia gigantea.* Radial section showing bordered pits on the tangential walls of the spring wood. × 280.

As an exceptional feature, bordered pits may sometimes be found upon the tangential walls of the spring wood. This is especially noticeable at the ends of tracheids, and in rare cases it may apply to the entire extent of the wall. The most notable instance of this kind, because practically unique, is to be met with in *Sequoia gigantea* (Figs.

11, 12). Those spring tracheids which lie in direct contact with the summer wood of the previous year, often exhibit this feature with great prominence, but it may also extend radially through several successive tracheids. This is undoubtedly a primitive character, and in the one case cited it possesses some value for the purpose of specific differentiation, but in general terms, the occurrence of bordered pits in such positions is of so sporadic a nature as to give this feature no well defined value, either for taxonomic or phylogenetic purposes. It may, nevertheless, be stated with respect to the pits on the tangential walls of the tracheids in general, that in their distribution they distinctly conform to the law governing similar structures on the radial walls.

Reference to *Cordaites acadianum* shows that in the multiseriate pits of the hexagonal form, these structures always preserve the spiral arrangement characteristic of the structures from which they were derived (Fig. 4), and this conformity also extends to the direction of the spirals which generally ascend from left to right. The general law in this respect has already been formulated so fully by De Bary (9, p. 163), as to make it unnecessary at this time to enter upon its consideration more in detail, beyond a reference to one or two special features and some apparently exceptional cases. While the spiral arrangement is always typical in such genera as Cordaites, Agathis, Araucaria, etc., it is not obvious in those cases where the pits are strictly uniseriate and often remote from one another. Nor is it apparent at first sight in those cases of 2-seriate pits where, as in *Cupressoxylon dawsoni* from the Cretaceous, *Larix americana*, Sequoia and various species of Pinus, the pits are always paired off in such a way that the axis of each pair is at right angles to the axis of the cell (Fig. 7). Two explanations are here possible: (1) the spirals are in reality 2-seriate, and they are projected through the alternate members of the two rows of pits, or (2) the disposition of the pits represents an extreme phase in the flattening of the original spirals conformably to a higher type of development. This latter view, which seems the more reasonable, is in direct harmony with De Bary's law, while it receives additional support from the form and direction of the pit orifice.

The orifice of the pit is variable, at different times being round, when the pits are also round and more or less distant; oval or oblong, when the pits assume corresponding forms; or in the summer wood, lenticular or oblong. The transversely elliptical pits of *Pinus strobus* (Fig. 8), the orifice of which is also transversely oblong, as also the similar pits of Pinus cubensis (Fig. 7), afford substantial proof in confirmation of the probable correctness of this view. In the summer wood, the pit orifice commonly assumes a position which appears to offer a direct contradiction of this conclusion. In *Pinus strobus* (Fig. 9), the orifice is oblong and parallel with the tracheid axis. In *Pinus pungens*, as in many others of the same genus (Fig. 13), the narrow orifice is extended above and below into a diagonal slit of great length, forming a narrow angle with the tracheid axis. At first sight this would seem to imply that these features represent primitive spirals, the original direction of which has not been greatly if at all modified, but one or two considerations will assist us to a correct interpretation of this feature. In the first place it is to be observed that such positions and modifications of the orifice are invariably associated with the summer wood, or where they occur in the spring wood, it is the result of maceration and commonly occurs in fossil plants, or woods in process of decay, and they are always most conspicuous in those tracheids which have experienced the most profound modifications with respect to the growth in thickness of the secondary walls. It has already been shown in the case of Taxus and Torreya, that there is no necessary connection between the spiral bands and the spiral lines of striation — that, as a matter of fact, as particularly illustrated by *Torreya taxifolia*, the two are quite distinct from one another under ordinary conditions of development. But in cases where the wall experiences extreme growth in thickness, the obliteration of the original spiral structure is complete, and at the same time it is replaced by the normal striation of the wall which,

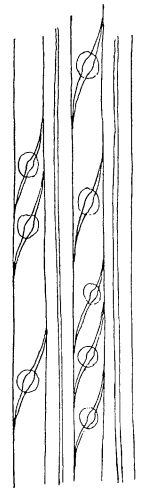


FIG. 13.—*Pinus pungens*. Bordered pits on the radial walls of the summer wood. × 280.

in such cases becomes most pronounced. Instances such as those afforded by *Pinus strobus* and *P. insignis* may, according to this interpretation, be held to represent the final phases in the obliteration of the original spirals, and they therefore constitute characters indicative of the highest type of development. In a few cases the structure of the bordered pit presents exceptional forms. In *Cupressus nootkatensis* the pit orifice shows either unusual want of regularity in outline and marked eccentricity of position, or it is so enlarged as to leave only a narrow border to the round or oval pit (Fig. 14). Similar features occur occasionally in other genera, and they are generally conspicuous in *Pinus tæda*. De Bary (9, p. 159) has directed attention to the same feature in Ephedra and *Pinus sylvestris*, and he correctly interprets it as a form of arrested development. Alterations also arise as a feature of secondary growth in those cases in which the wall acquires unusual thickness. This is typically the case in *Pinus cubensis* where in plan (Fig. 15), the orifice is extended vertically to a length often twice the diameter of the original pit. In tangential section, according to the particular direction of the plane of section (Fig. 16), the orifice is either of uniform width, or it enlarges constantly through the entire thickness of the later growth, from within outwards. That such unusual forms are features of extreme, secondary growth of the wall, and that they may be anticipated in all cases where such modifications of the walls occur, is a reasonable deduction from the observed facts.

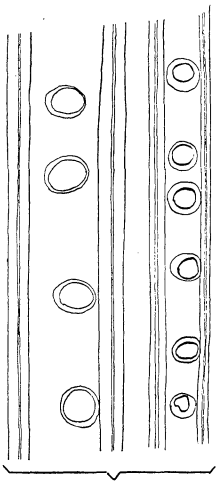


FIG. 14.—*Cupressus nootkatensis*. Radial section showing deformed bordered pits. × 280.

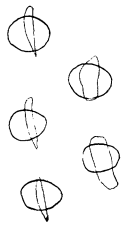


FIG. 15.—*Pinus cubensis*. Radial section showing deformed bordered pits. × 280.

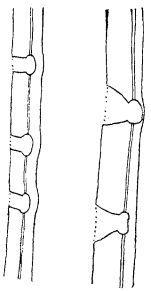


FIG. 16.—*Pinus cubensis*. Tangential section of bordered pits as in Fig. 15. × 280.

Taxonomic and Phylogenetic.

For taxonomic purposes, the bordered pits possess a definite though often limited value. In the genus Cordaites, as also in Araucarioxylon, Araucaria and Agathis, this is expressed in the hexagonal form together with their very compact, chiefly multiseriate arrangement throughout the entire extent of the tracheids, — characters which are of generic value and at once serve to separate these genera from all others. The contrasting differential feature is then to be found in the pits of the oval or round form, together with their 2-seriate or 1-seriate disposition with a more or less marked tendency to segregation. This is characteristic of the Ginkgoales and all the Coniferales, both fossil and recent.

As a different character of sub-generic value, the occurrence of bordered pits on the tangential walls of the summer wood of the first section of Pines — the soft pines — and their invariable absence from the same structural region in the second section — the hard pines, — is one which may be always relied upon.

For the purposes of specific differentiations, the pits on the tangential walls possess a distinctly inferior value which must be confirmed in most cases by the evidence of other factors. Their utility in this respect is made sufficiently clear in the various diagnoses and in the artificial key, without further discussion at this time.[1]

In the genus Cordaites, according to the provisional specific differentiations of fossil forms as at present generally employed, the number of rows of pits, or their segregation into definite groups, are characters of well defined, specific value, since they are among the few features which may be utilized with certainty for this purpose. Thus *C. acadianum* with its 2–5 rows; *C. materiarium* with 2–4 rarely 3–4 rows; *C. hamiltonense* with two rows and *C. newberryi* with two rows in groups of 6–13 pits, rest upon a basis which is not only easy of recognition, but which may be applied with full assurance, as has been done

[1] This paper will appear in the *Trans. Royal Society of Canada* for 1904.

on former occasions (38, p. 51 et seq.) In Araucaria, the three species investigated may be similarly differentiated from one another. The same rule is applicable to *Torreya taxifolia* which is thereby separable from the other species; likewise to *Cupressoxylon dawsoni*, *Tsuga canadensis*, *Larix americana*, and, among the pines, *P. lambertiana*, *P. clausa*, *P. sabiniana*, *P. tæda*, *P. palustris*, and *P. cubensis*. It is to be observed, however, that the constancy which characterizes this feature in Cordaites and Araucaria, is wanting in the higher Abietineæ. In Larix there is such variation that very careful scrutiny is required, while in the genus Pinus, the number of exceptions to the typical character increases greatly, and is liable to cause some difficulty in the final determinations unless much care is exercised. *Pinus tæda* offers a conspicuous illustration of this fact, as may be seen by reference to the analytical key. It is therefore manifest that the value of the bordered pits for taxonomic purposes is most clearly defined in the lower types of the Coniferales, and that their value diminishes steadily, with an advance toward higher forms of organization and development. In all cases where exceptional forms introduce diagnostic difficulties, these may be overcome by the controlling effect of associated characters.

We are now in a position to examime the data at hand with a view to determining the bearing of the bordered pits upon questions of phylogeny.

Having reference to the origin of the bordered pit and the various modifications it presents in the course of development, it cannot be doubted that the hexagonal, multiseriate pits of Cordaites, Araucarioxylon, Araucaria and Agathis place those genera in a relatively inferior position, a view which gains a large measure of support from the well known and extensively multiseriate disposition shown in *Heterangium grievii* (49, p. 341), but the facts so far discussed have not as yet thrown any special light upon the relative positions of the separate genera.

An examination of twelve species of Cordaites shows that the bordered pits exhibit a much wider range of serial variation than any other genus covered by the present studies. If then we accept the general principle with respect to the development of the bordered pits as already illustrated, it cannot be doubted that

the 2–5-seriate pits stand much nearer to the primitive form of the tracheid than do the 1-seriate. From this point of view it is then evident that in *C. recentium*, the name of which is thereby seen to be fully justified, the 1-seriate pits place it at the upper end of a series which has its inferior termination in the 2–5-seriate *C. acadianum*, while between the two, intermediate forms appear as members of a series of nine variants, and it is possible to arrange these in such a manner as to exhibit the probable sequence in development as follows:—

Serial variations in the Bordered Pits of Cordaites.

	2–5 ser.	3–4 rarely 2.	2–4 chiefly 3.	3–4 chiefly 2.	2–3 rarely 4.	2–3 chiefly 2.	1–3 chiefly 2	2-ser.	1-ser.
C. acadianum	x								
ohioense		x							
ouangondianus			x						
materiarium				x					
clarkii					x				
annulatum						x			
brandlingii							x		
materioide							x		
illinoisense							x		
hamiltonense								x	
newberryi								x	
recentium									x

The wide range of variations here shown, especially when compared with other genera, at once serves to suggest that Cordaites was in this respect somewhat of the nature of a transition group from which others were given off, or else that it epitomized the collective changes through which a number of genera must have passed. And inasmuch as this genus exhibits a more highly developed, multiseriate arrangement than any other within the general phylum, we must concede that it is, with respect to this character, the most primitive of all.

The genus Araucaria shows a much more restricted range of variations, there being only four variants pretty uniformly distributed among fourteen species, both recent and fossil. While the most highly developed members, four in number, are represented by 1-seriate pits, the most primitive form of 4-seri-

ate pits occurs in only one case — *A. robertianum*. It is therefore manifest that this genus is obviously of a more advanced type than Cordaites from which it undoubtedly originated. Agathis being represented by only one species, it is not possible to locate it more definitely than to say that the 1–3-seriate disposition of its pits would place it in a position equivalent to that occupied by *Araucaria cunninghami* and therefore about three-fourths way down the scale for that genus. This fact points with much force to the idea that of the two genera, Agathis is of relatively lower type.

The Ginkgoales and the Coniferales as a whole, exhibit an obviously higher type of development than the preceding group, in consequence of the more pronounced tendency to segregation of the pits which are now either elliptical or round, and never hexagonal. This distinction is so clearly defined and constant as to support the idea which gains force in other ways, that Cordaites, Araucaria and Agathis are clearly related members of a principal branch of the original stock, and that they therefore diverge considerably from the particular line of descent within which we find both the Ginkgoales and the Coniferales.

The observations so far made apply altogether to the pits on the radial walls. We may now pass to a consideration of their relation to the tangential walls, a factor which does not call for very extended discussion. This feature is found to apply to 71.7 % of all investigated species exclusive of fossils. It is wanting in three species of Araucaria, representing 2.58 %; in Torreya, 2 species or 1.72 %, and in the entire second section of Pinus to the extent of 28 species or 24.1 %. But the occurrence of pits on the tangential walls, in common with those on the radial walls, is a well known feature of the Sigillarias (49, p. 198), where their primitive character is well established, and we can hardly doubt that their ultimate elimination in the higher pines is the expression of a final phase in development, consistent with the position usually assigned those plants. The absence of pits from the tangential walls of certain Araucarias and Torreyas, is to be interpreted as one of those sporadic tendencies toward a higher type of development which never become permanent in the same line, but which are to be met with as one of the invariable features of evolution.

Ginkgo, being the unique representative of an ancient line, cannot very well be brought into the present discussion very much in detail. On other grounds it is known to be a primitive form representing a group distinctly inferior to the Coniferales, and this view is supported by the disposition of the pits in two series, a character which, if taken alone, would give the genus rank with *Torreya taxifolia* among the Taxaceæ, but when regarded collectively, would place the genus distinctly below the Coniferales as a whole. This evidence, then, indicates that the Ginkgoales must have arisen as a side line at some point inferior to the Coniferales, but superior to the Cordaitales.

In the Taxaceæ the bordered pits do not in themselves afford very conclusive evidence as to the relative position of the family. Among the eight investigated species, representative of three genera, only three, and chiefly two variants occur. Taken alone, the disposition of the pits would lead to no final conclusion, but other factors permit of placing this family in the inferior position usually assigned to it. Within the genus three variants are found — the 1–2 rows of *T. taxifolia*, the one row or pairs of *T. californica* and the strictly 1-seriate form of *T. nucifera*. In Taxus only two variants appear — the one row or pairs of *T. floridana* and the 1-seriate disposition as found in the remaining three species. The one representative of Podocarpus shows but one variant, and that is 1-seriate. From this it is obvious that the generic sequence must be in the order given, and that the sequence of species must be approximately as given in the table of anatomical data to follow.[1]

The remaining genera of the Coniferales present so few deviations from a typical form, that they cannot be differentiated fully on the basis of the bordered pits. This character nevertheless has a definite value in association with others, as in the genus Sequoia or some of the hard pines, *Larix americana*, etc. The general sequence of genera may be recognized by the bordered pits only in so far as these structures serve to confirm and emphasize the conclusions reached in other ways, and this will become apparent from an inspection of the table of anatom-

[1] This table will appear in the last number of this series.

ical data. It will nevertheless serve a useful purpose at the present moment, to ascertain the general sequence based upon the percentage distribution of the principal variants as follows.

Comparison of the principal variations in the serial arrangement of bordered pits, by percentages.

	Total var.	2–5	2–4	2–3	1–3	2	1–2	1+ pairs.	1
Cordaites . .	9	8.3	25.0	16.6	25.0	16.6			8.3
Agathis . . .	1		6.6	20.0			40.0		33.3
Araucaria . .	4		6.6	20.0			40.0		33.3
Ginkgo . . .	1						100.0		
Sequoia . . .	1						100.0		
Larix . . .	3						33.3	33.3	33.3
Taxodium . .	2						25.0		75.0
Libocedrus . .	1							100.0	
Thuya . . .	1							100.0	
Pseudotsuga .	2							50.0	50.0
Pinus . . .	3						17.1	41.5	41.4
Abies . . .	3						13.6	27.3	59.1
Taxus . . .	2							25.0	75.0
Tsuga . . .	3						16.7	16.7	66.6
Picea . . .	2							10.0	90.0
Podocarpus .	1								100.0
Thujopsis . .	1								100.0
Cryptomeria .	1								100.0

With respect to specific differentiations, it has already appeared that the bordered pits may be employed with success in Taxus and Torreya. In Cupressus this rule also applies to *C. pisifera*, and *C. macrocarpa*, both of which are distinguished by having their pits in one row or pairs, while the remaining seven species have strictly uniseriate pits. An instructive example is afforded by *Cupressoxylon dawsoni*. In this species, which is of early Tertiary age (Lignite Tertiary), the pits are typically 2-seriate, being disposed in a very compact manner similar to that found in existing Sequoias. But in a series of eleven specimens, it is clearly seen that two variants are represented — the second being a 1-seriate form. These variations are also found, as in the other Coniferales, to be directly related to variations in the size and rate of growth of the tracheid. It cannot be doubted then, that *C. dawsoni* is a more primitive representative

than any species now existing, and that it is substantially the ancestral form of the genus, so far as we know.

In Larix the four investigated species may be differentiated pretty fully, and this rule applies with particular force to *L. americana*, and *L. occidentalis*, both of which are distinguished by a 2-seriate form. Among the pines, *P. lambertiana*, *P. clausa*, *P. sabiniana*, *P. tæda*, *P. palustris*, and *P. cubensis* are readily differentiated from the others by the 2-seriate pits. In all other cases than those specifically indicated, the bordered pits afford an inadequate basis for specific differentiation.

It is now apparent that segregated, round or oval pits in one row must be taken as representing the highest type of development in the Coniferales, and any deviation from this must be taken to indicate the survival of more primitive conditions, pointing to derivation from a type like that of Araucaria or Cordaites. From this point of view, the occurrence of pits in 1–2 rows in *Larix americana*, *Torreya taxifolia*, Sequoia, *Tsuga canadensis* and various species of Pinus, indicates the survival of ancestral characters which are partial to the extent of 7.2 %, and complete to the extent of 10.8 %. That such deviations from the usual type of structure are either survivals or reversions which serve to indicate a common origin, cannot be doubted, more especially as they do not occur at a fixed point near the original type, but they arise sporadically in widely separated genera. The tendency of such evidence then, is to show a common ancestry for the various genera of the Taxaceæ and Coniferæ, a view which is greatly strengthened by the testimony afforded by the spiral tracheids of *Larix americana*, Pseudotsuga and *Pinus tæda*. The provisional conclusions which we now reach are, that there were probably four main lines of descent from the original stock represented by Cordaites:

1 Araucaria and Agathis.
2 Ginkgoales.
3 Taxaceæ.
4 Coniferæ.

(*To be continued.*)